

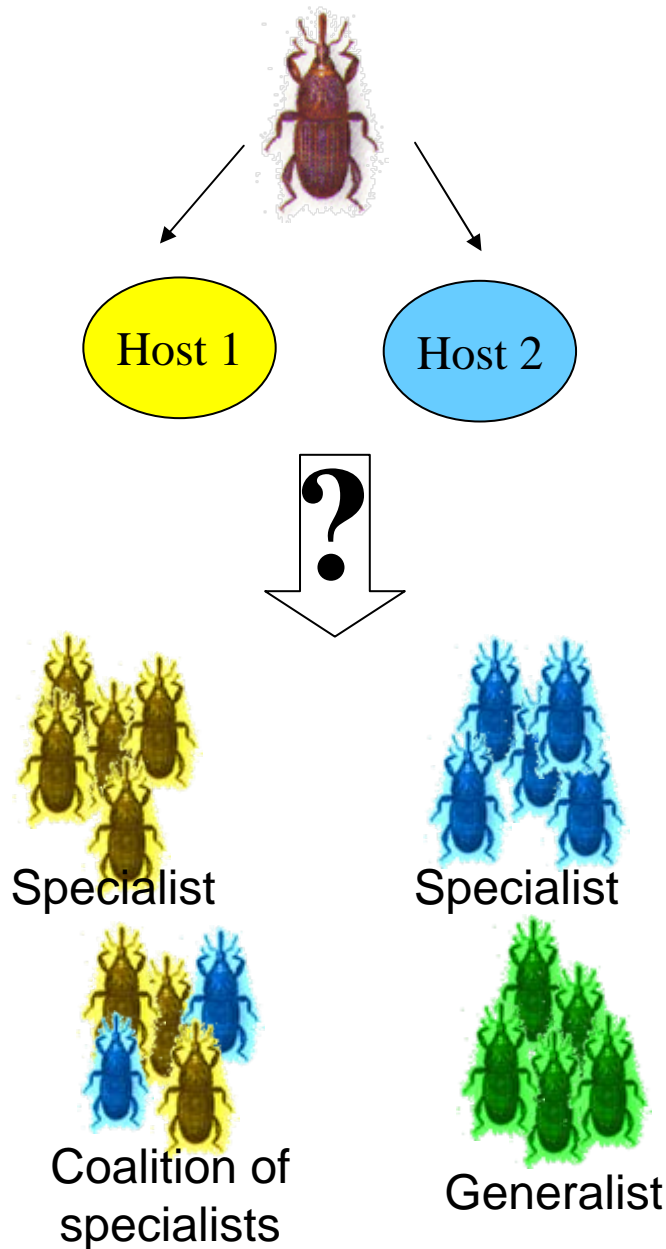
Specialization as a joint evolution of host choice and local adaptation

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Speciation and specialization in parasites



Speciation requires a source of disruptive selection

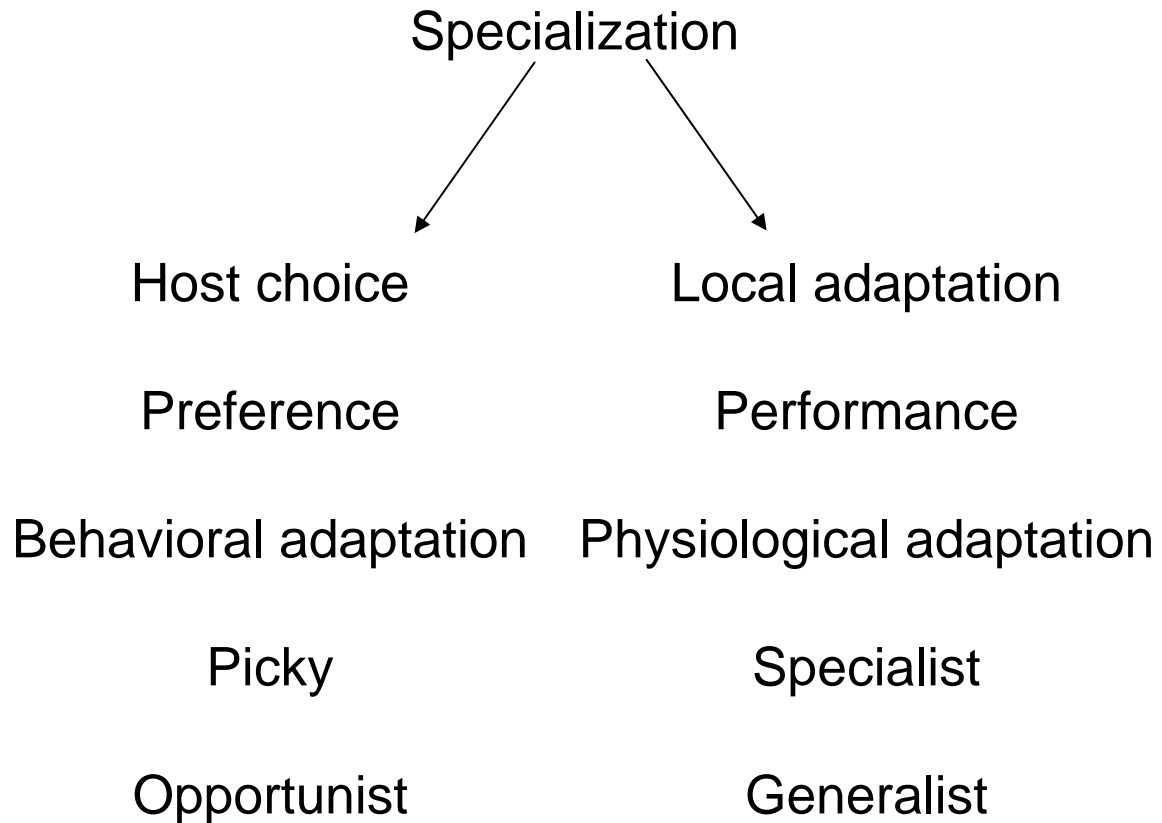
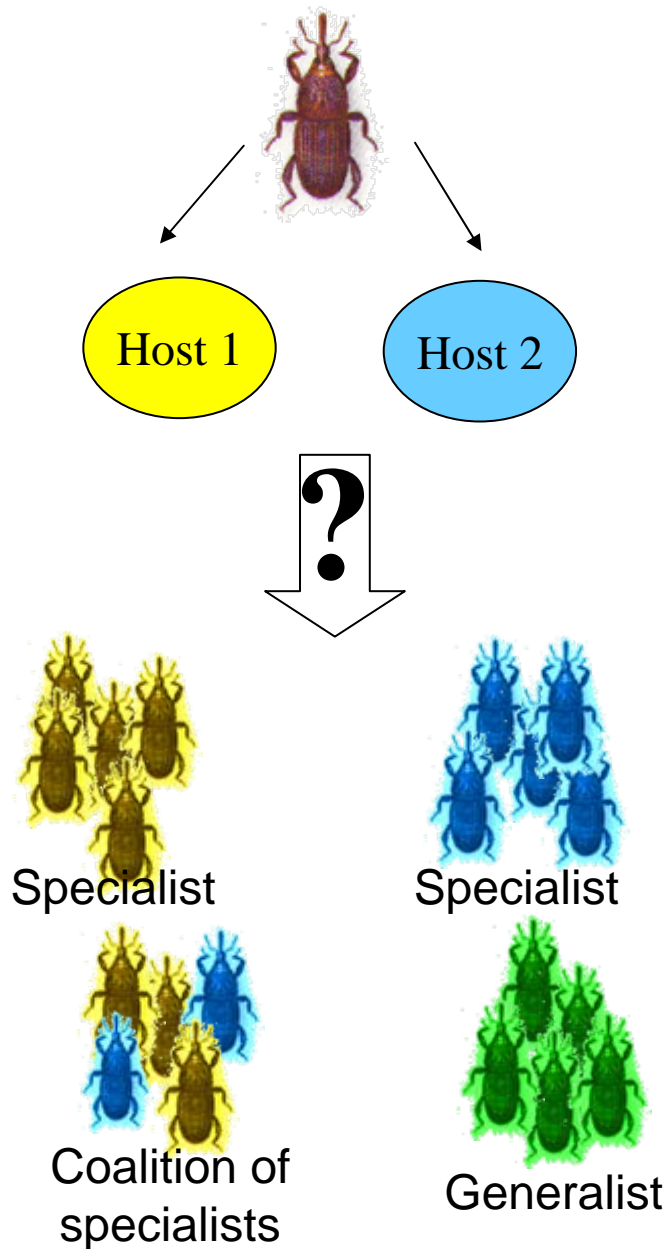
Host diversity may be an important source of disruptive selection in parasites

When does host diversity favor specialization ?

When does specialization associates with parasite diversification ?

When may reproductive isolation evolve ?

Host choice and local adaptation

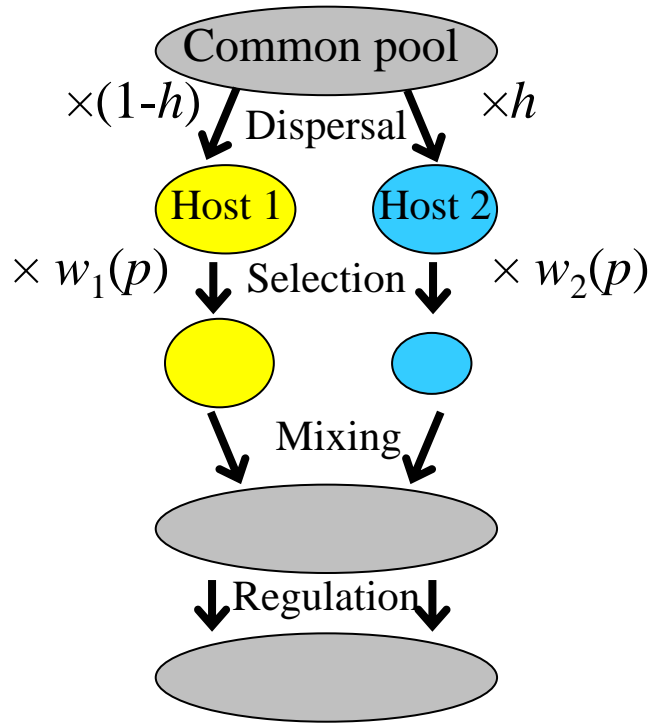


Ingredients of a general but simple model of specialisation

- Two hosts (1 and 2) and a (clonal) parasite population
- A local adaptation trait p that determine local fitness (fecundity or survival within each host) : $w_1(p)$ and $w_2(p)$
- How individuals distribute among hosts is controlled by a host choice trait h (proportion of individuals in host 2 after dispersal stage)
 - may be the result of complex choice mechanisms
- Population density regulation

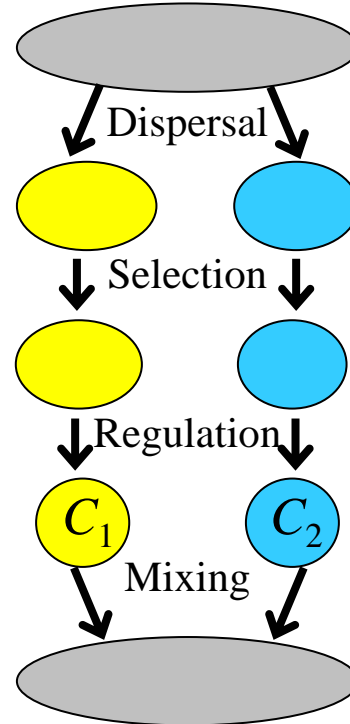
Three simple life cycles combining dispersal, selection and regulation

Dempster 1955



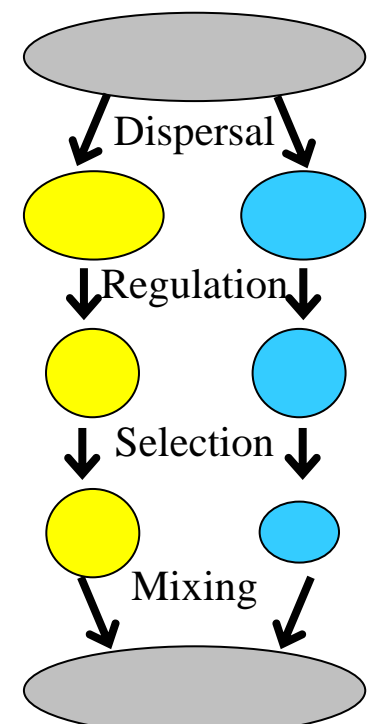
Hard selection

Levene 1953



Soft selection

Model 3



Local
regulation

Global
regulation

Variable
output

Model 3

Dempster

Constant
output

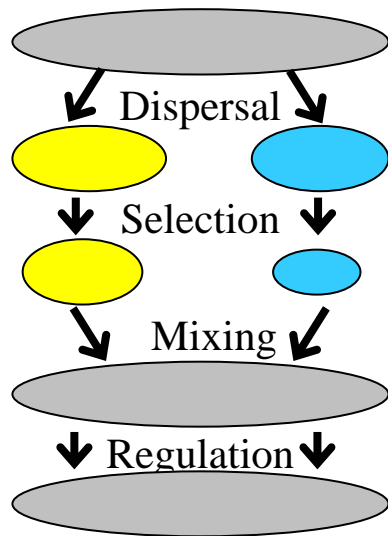
Levene

Infeasible

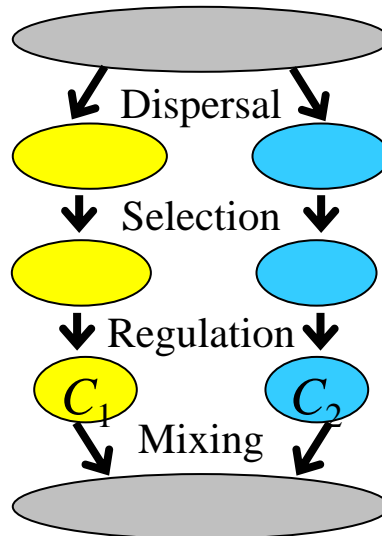
Resident parasite population : p, h, N

Mutant parasite population : $p_m, h_m, N_m(t)$

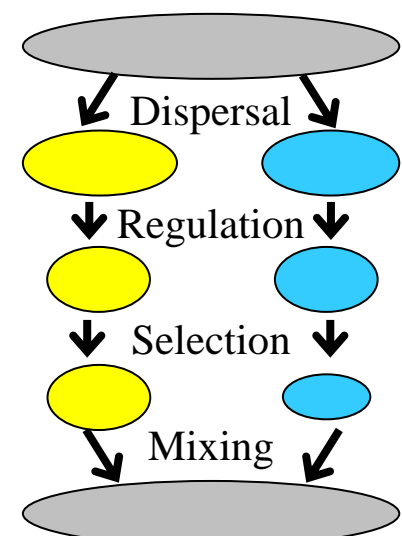
Hard selection



Soft selection



Model 3

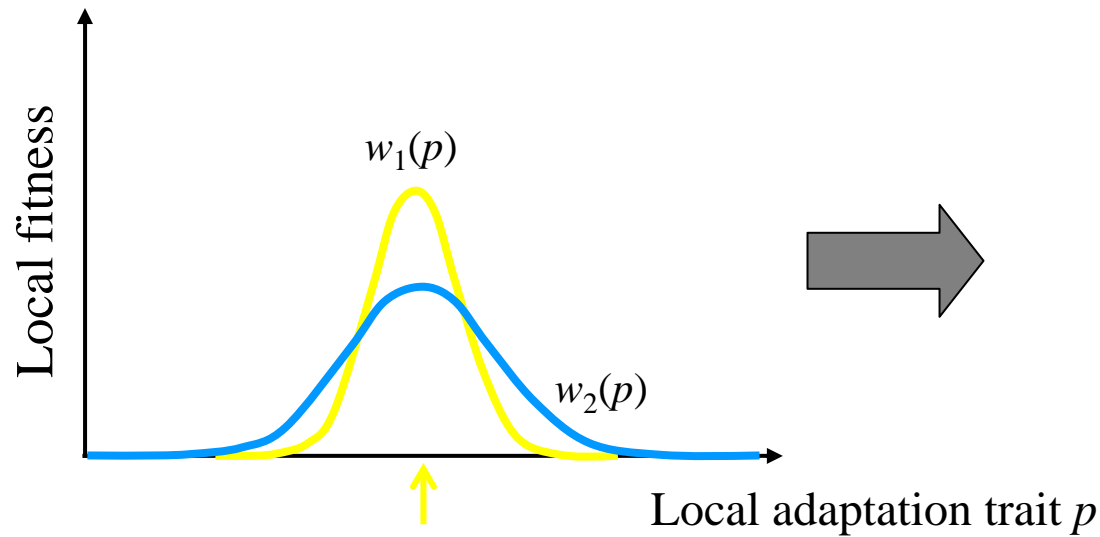


$$s_{p,h}(p_m, h_m) = \ln \left(\frac{(1-h_m)w_1(p_m) + h_m w_2(p_m)}{(1-h)w_1(p) + h w_2(p)} \right)$$

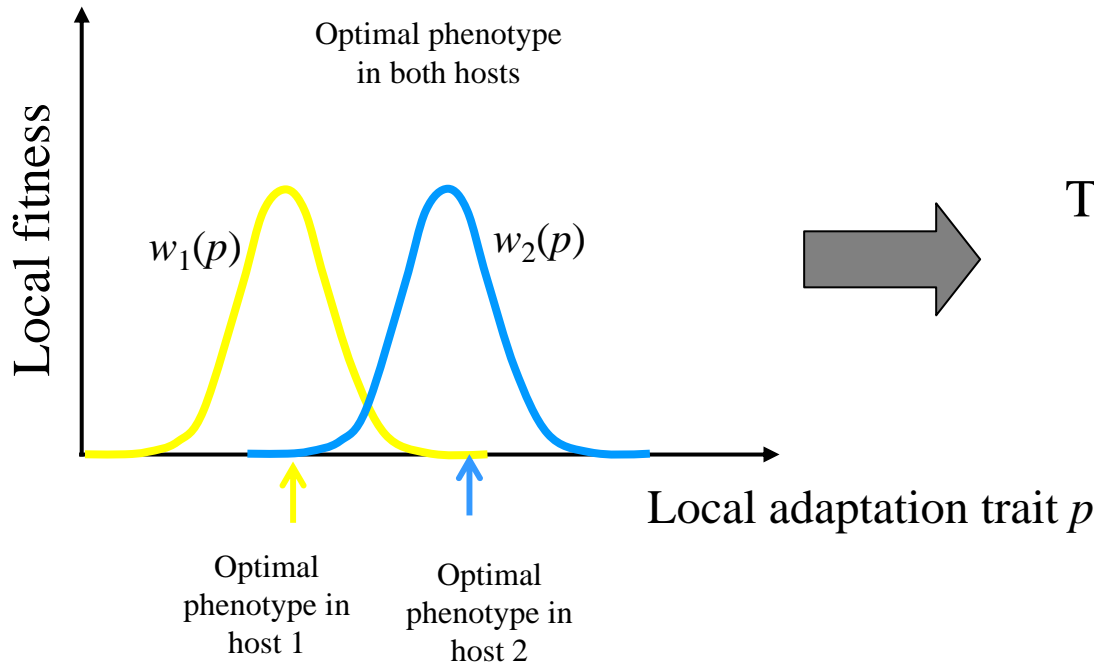
$$s_{p,h}(p_m, h_m) = \ln \left(c_1 \frac{(1-h_m)w_1(p_m)}{(1-h)w_1(p)} + c_2 \frac{h_m w_2(p_m)}{h w_2(p)} \right)$$

$$s_{p,h}(p_m, h_m) = \ln \left(\frac{c_1 w_1(p_m)}{c_1 w_1(p) + c_2 w_2(p)} \frac{1-h_m}{1-h} + \frac{c_2 w_2(p_m)}{c_1 w_1(p) + c_2 w_2(p)} \frac{h_m}{h} \right)$$

Evolution of local adaptation - Something trivial



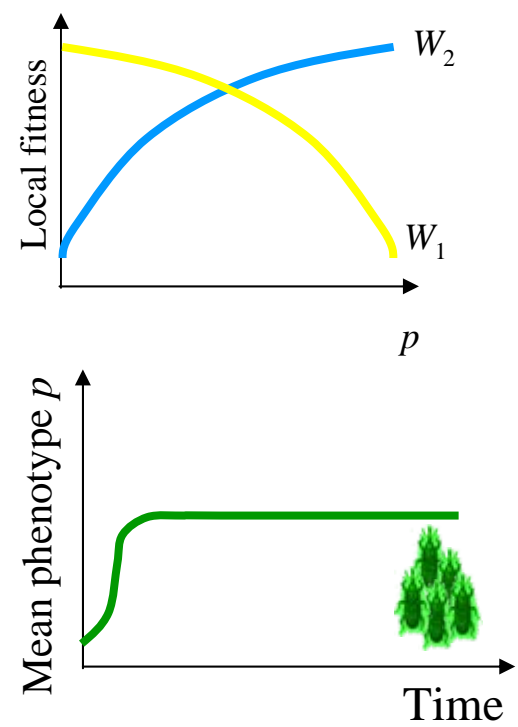
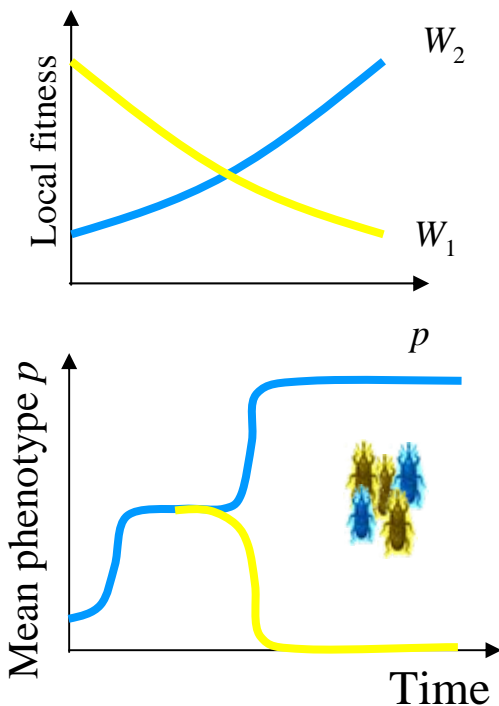
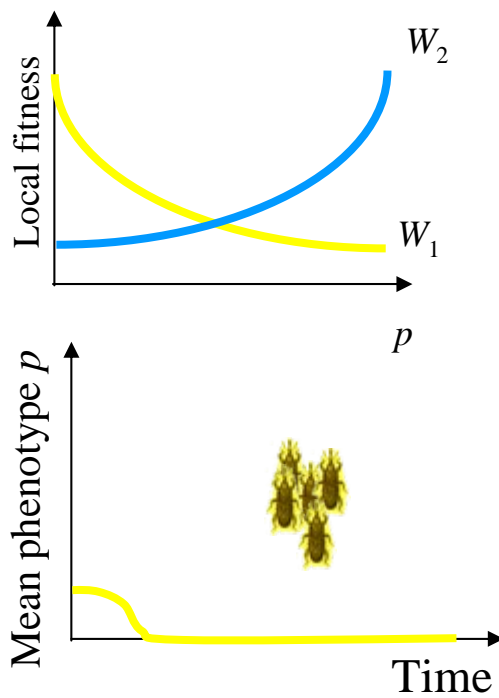
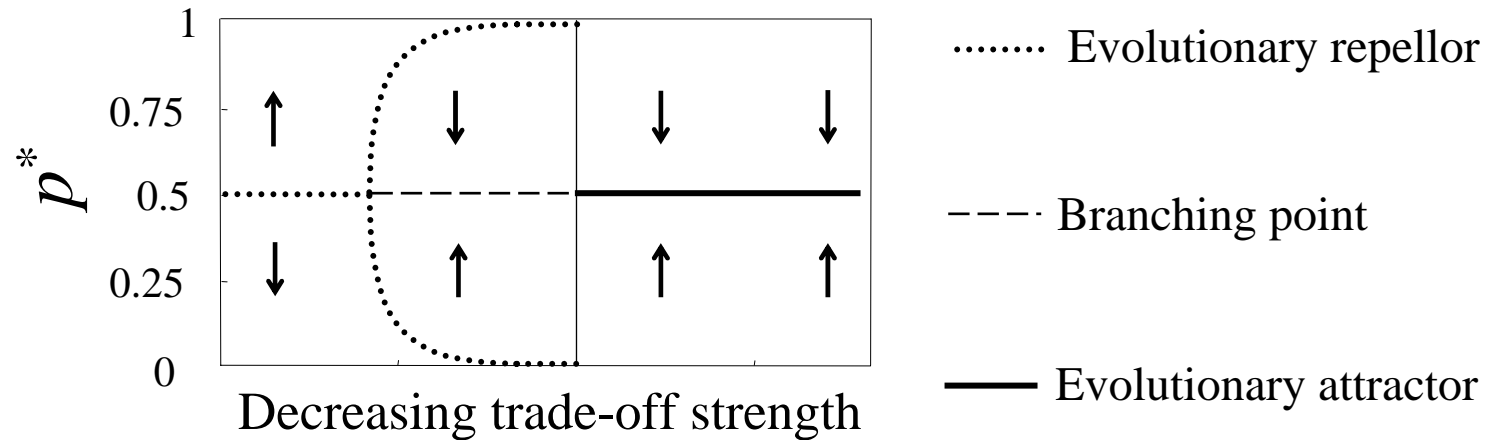
Stabilizing selection toward optimum – no selection for specialization



Trade-off in local adaptation to both hosts – there exists a singular strategy

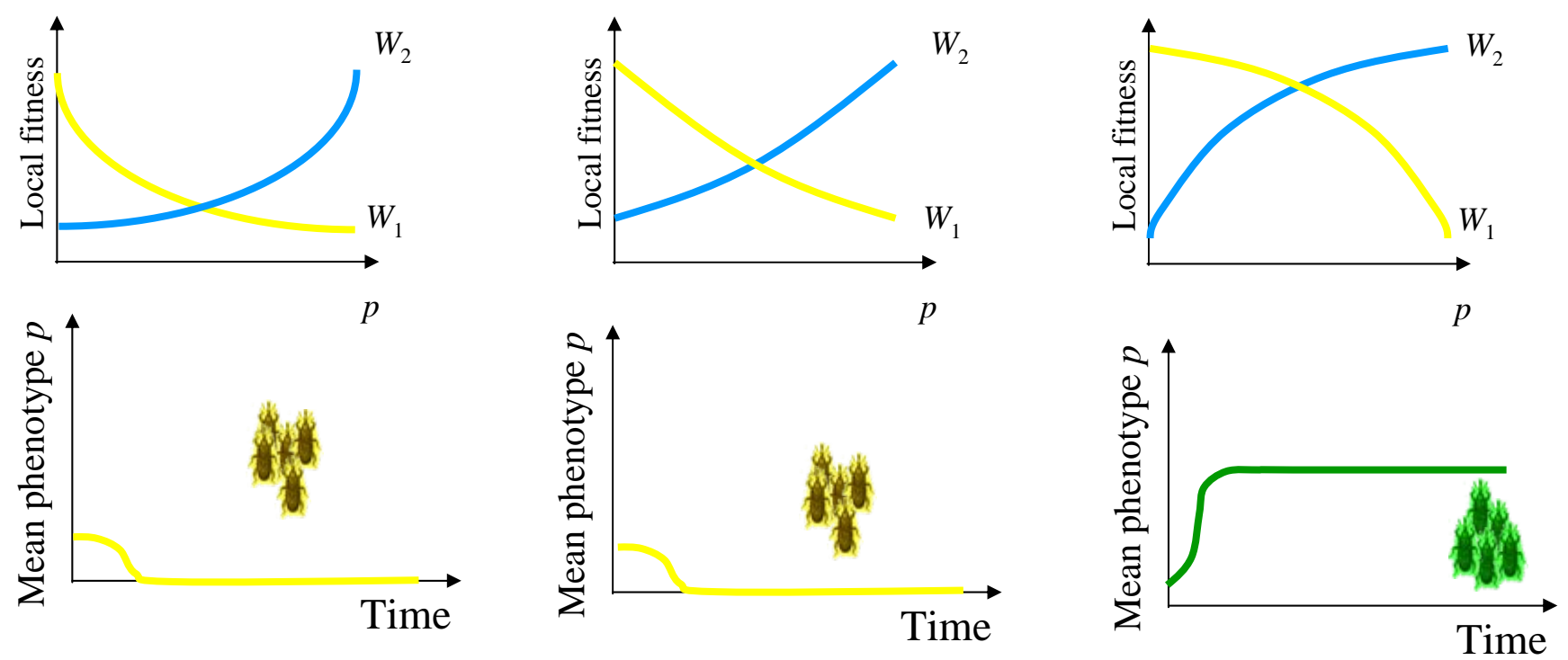
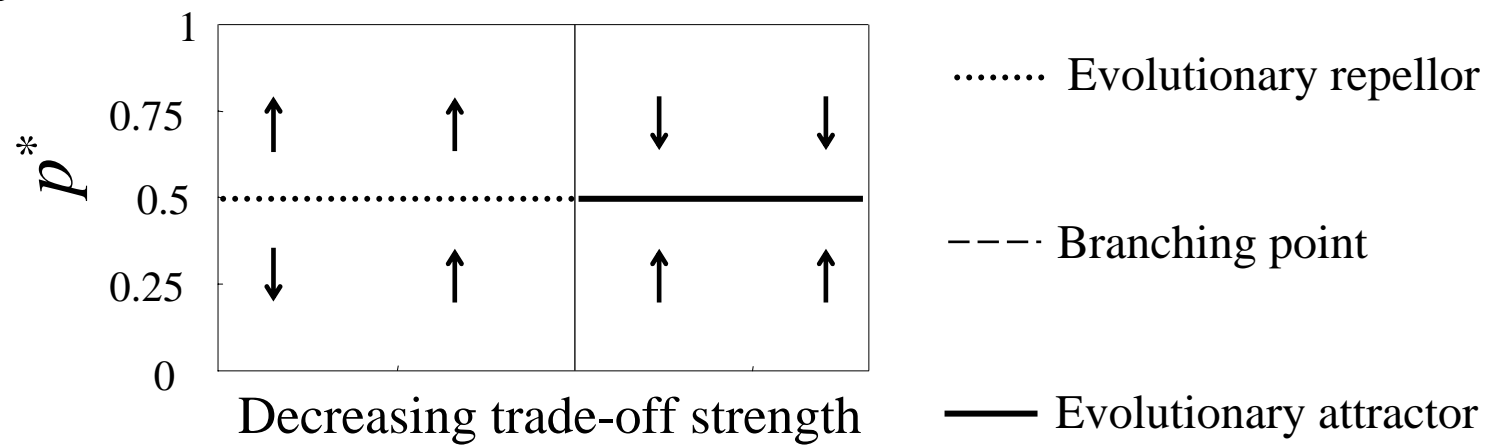
Evolution of local adaptation – Soft selection – Constant host output

Symmetric



Evolution of local adaptation – Hard selection – Variable host output

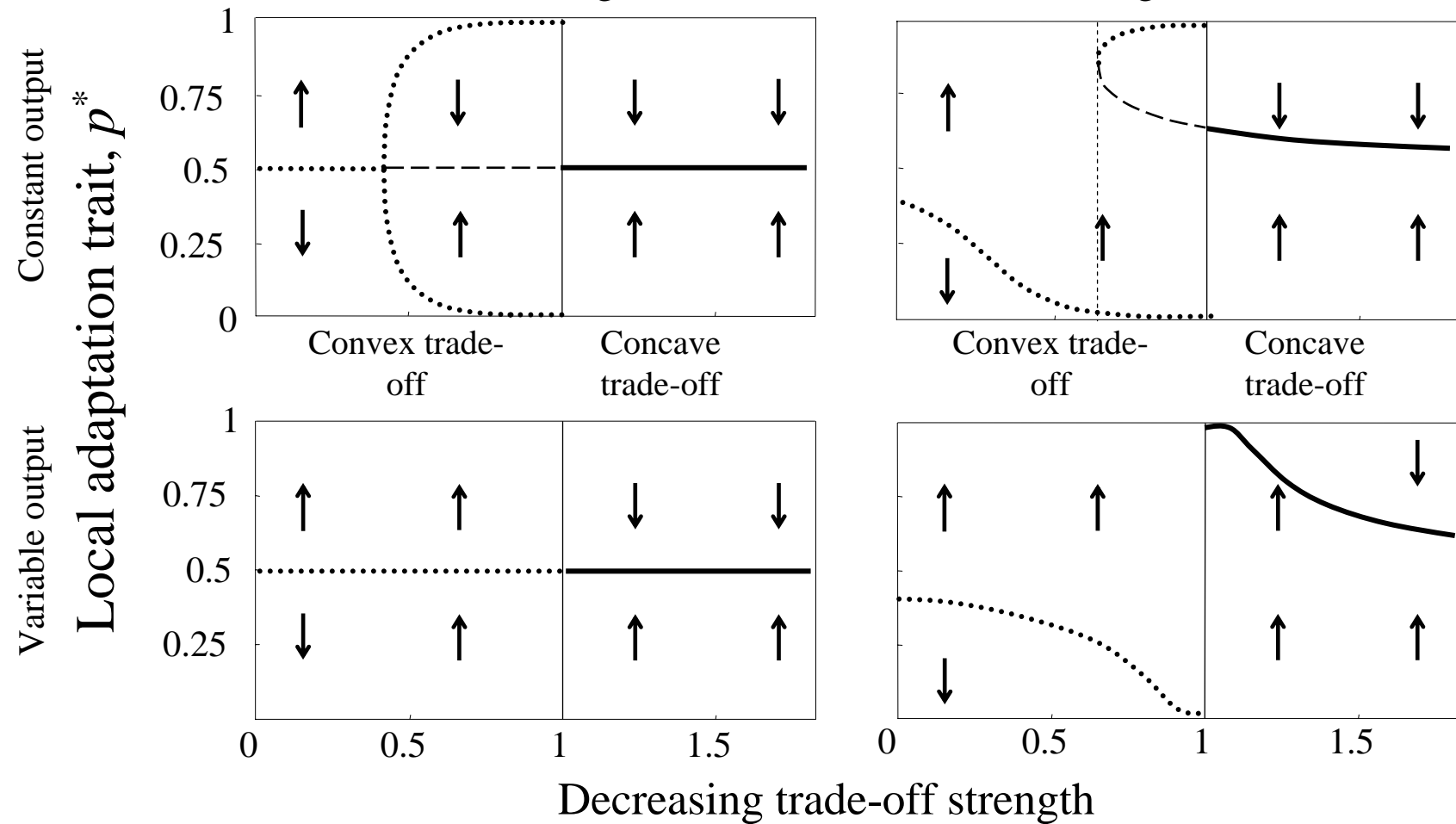
Symmetric case



Evolution of local adaptation

Symmetric distribution of individuals among habitats

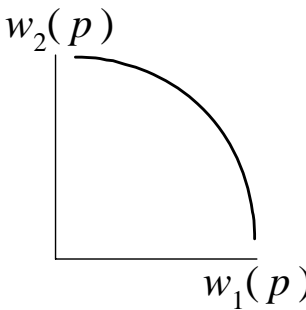
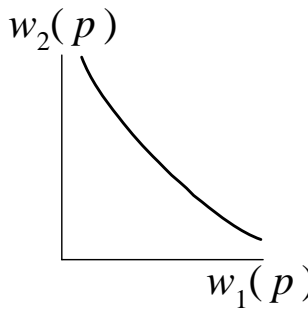
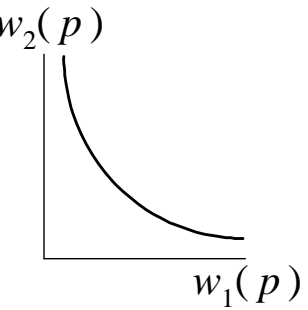
Biased distribution of individuals among habitats



..... Evolutionary repellor

---- Branching point

— Evolutionary attractor

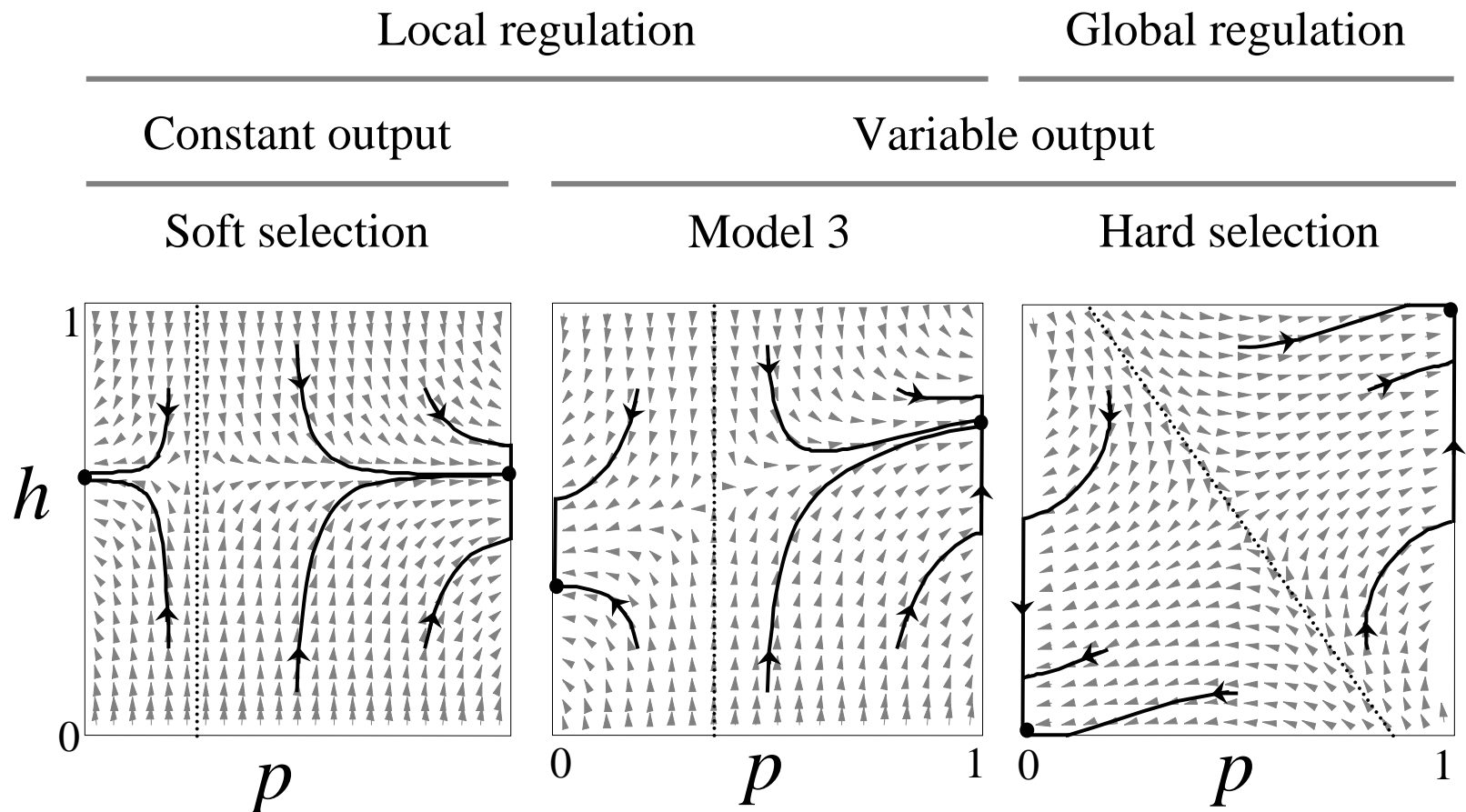
Local adaptation trade-off	 <p>Concave trade-off</p>	 <p>Slightly convex trade-off</p>	 <p>Very convex trade-off</p>
Evolution of local adaptation under fixed and unconditional habitat choice			
Constant host output (Soft selection)	Evolutionary attractor 1 intermediate local adaptation phenotype	Branching 2 specialists	Bistability 1 specialist
Variable host output (Hard selection and Model 3)			

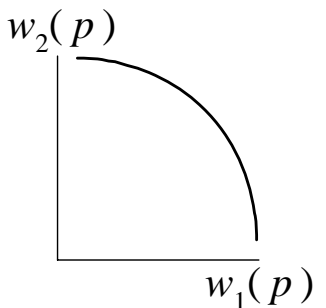
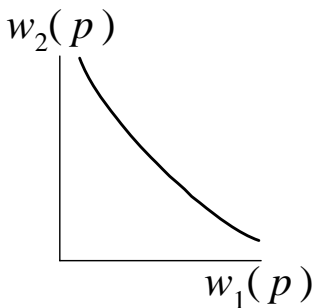
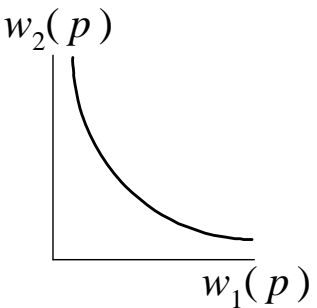
Evolution of host choice alone

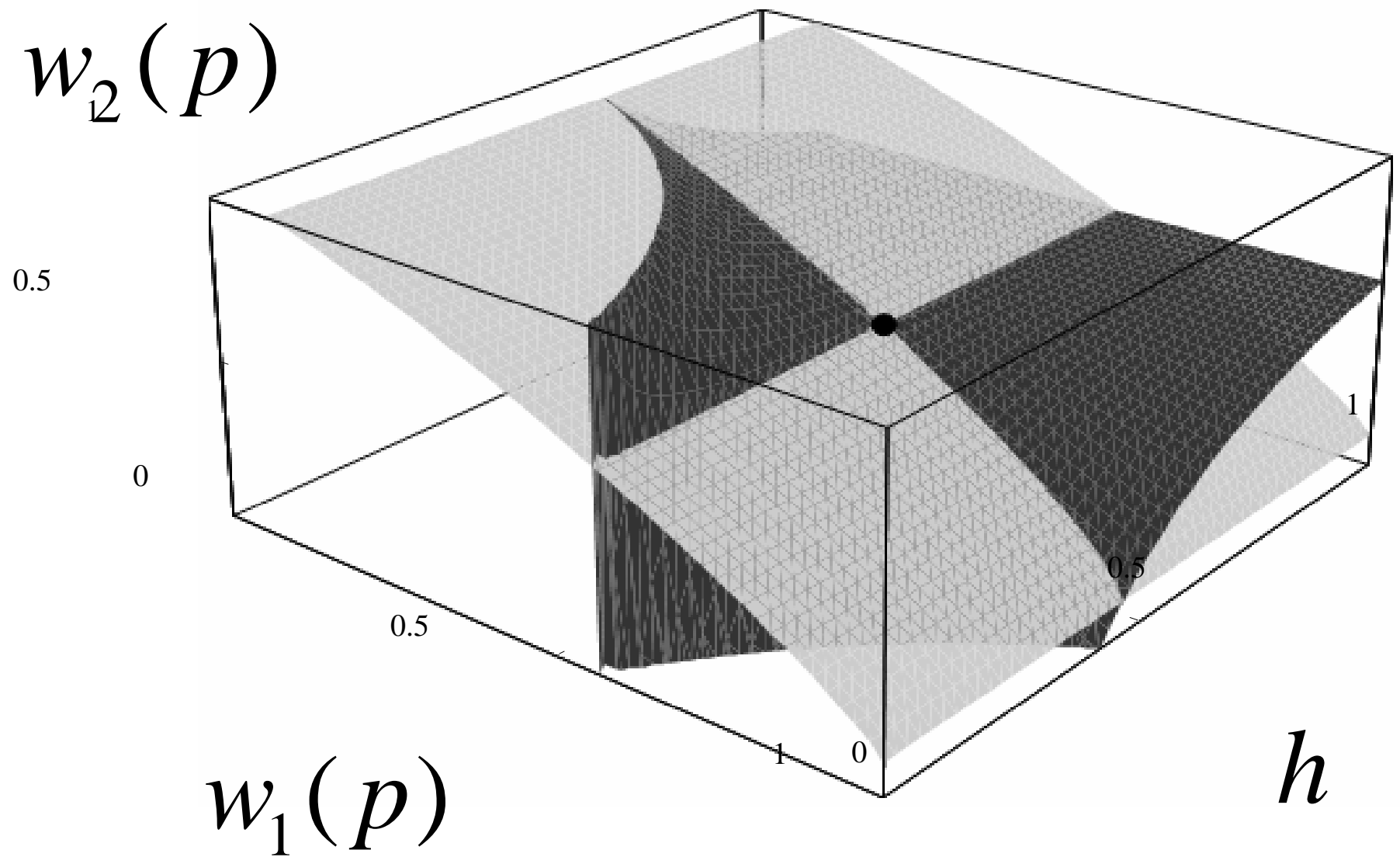
Local regulation		Global regulation
Constant output	Variable output	
Soft selection	Model 3	Hard selection
$h^* = c_2$	$h^* = \frac{c_2 w_2(p)}{c_1 w_1(p) + c_2 w_2(p)}$	$h^* = 0 \text{ or } 1$
Equal competition intensity among hosts (IFD)		

Joint evolution of host choice and local adaptation

- Only two possible outcomes :
 - branching and emergence of a coalition of two extreme specialists
 - bistability and emergence of a single specialist



Local adaptation trade-off	 Concave trade-off	 Slightly convex trade-off	 Very convex trade-off
Evolution of local adaptation under fixed and unconditional host choice			
Constant host outputs (Soft Selection)	Evolutionary attractor 1 intermediate local adaptation phenotype	Branching 2 specialists	Bistability 1 specialist
Variable host outputs (Hard sel. + Model 3)			
Joint evolution of local adaptation and host choice			
Constant host outputs (Soft selection)	Local regulation (Soft sel. and Model 3)	Branching 2 specialists	Bistability 1 specialist in ideal free distribution
Variable host outputs (Hard selection and Model 3)			
	Global regulation (Hard sel.)	Bistability 1 specialist leaving an empty niche	



Host choice evolution → no generalist

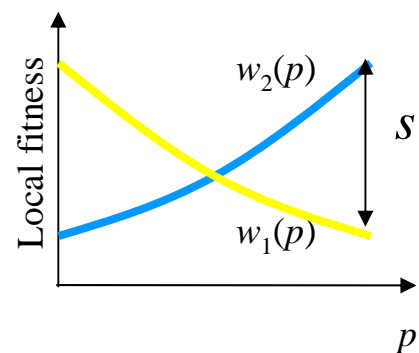
- no temporal variability
- no cost of choosiness
- no constraints (e.g., time limitation)

More realistic population dynamics

- are surprisingly well captured by these qualitative considerations on local vs. global regulation and constant vs. variable output

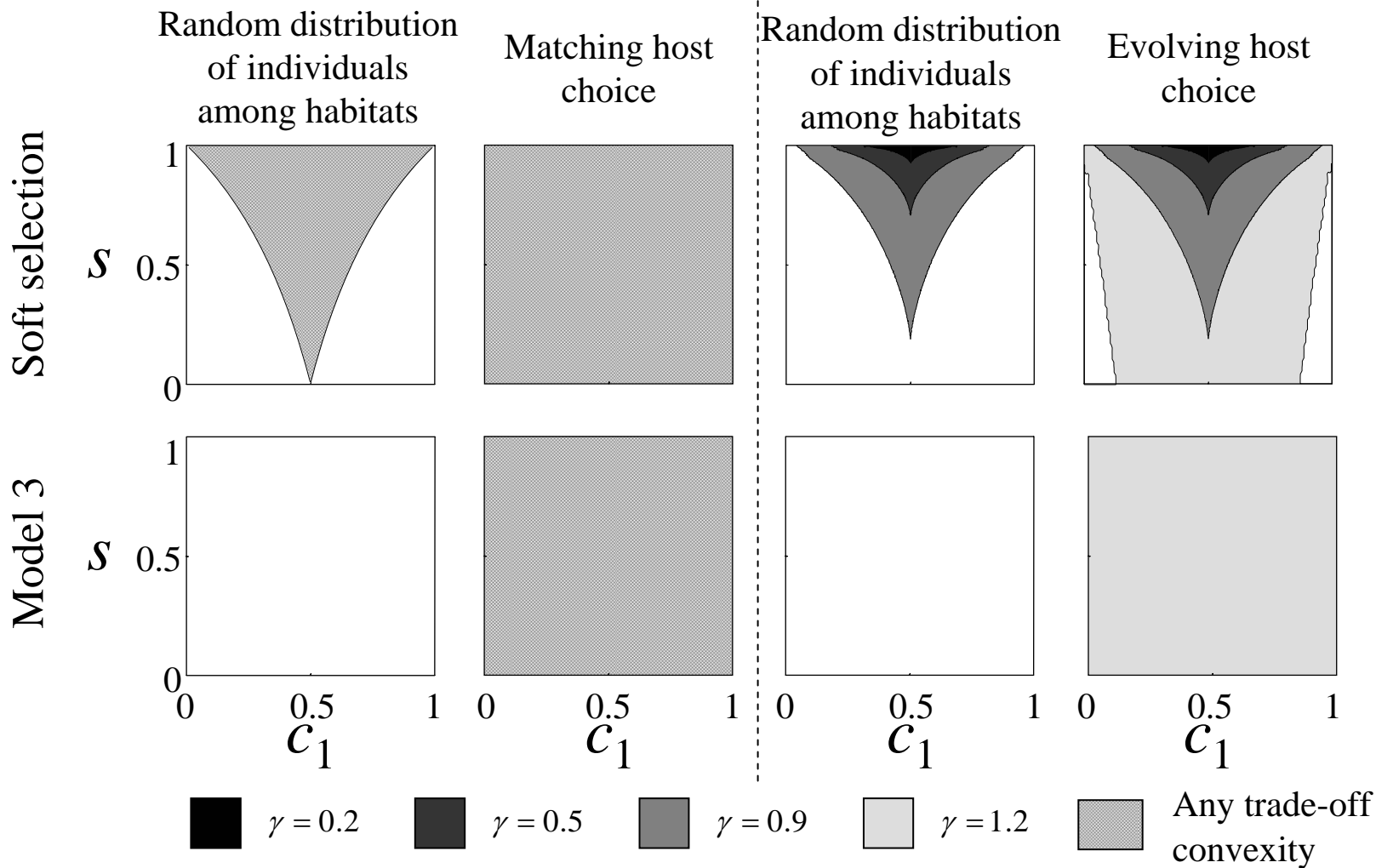
Evolution through small mutations steps

→ discrepancy with population genetics analysis of these life cycles



Maintenance of local adaptation polymorphism

Emergence of polymorphism through small mutations steps



Larger mutation steps = Lesser importance of trade-off shape

Importance of the genetic architecture of local adaptation
and host choice

e.g., Hawthorne and Via 2001

Evolution of the genetic architecture of traits under selection
in heterogeneous environments

Thank you for your attention